

back it is fed from the left ovarian artery, it is necessary to divide the Fat-body between the two gonads. Thus it comes that the anterior part of the Fat-body is represented on the right side of the animal and the posterior part on the left. As the Anterior Abdominal Vein runs in the Fat-body it is also divided and is so represented in the diagram, in which its two ends are joined by a dotted line.

PLATE LXXI.

Diagrams of the Blood-vessels in the head of *Tropidonotus natrix*.

- Fig. 3. Diagram of the Cranial Arteries seen on the ventral surface of the brain. The brain is represented as removed from the skull leaving behind, however, the Pituitary Body.
- Fig. 4. Diagram of the arteries of the head seen from the dorsal side. The brain is removed, but some of the cranial arteries are left behind. The positions of the glands of the head are indicated by shaded areas.

PLATE LXXII.

- Fig. 5. Diagram of the vessels on the ventral side of the lower jaw after the removal of the superficial muscles.
- Fig. 6. Diagram of the Veins and Sinuses in the head seen from the dorsal side. The deeper vessels are represented in lighter shading and with a dotted outline. The position of the brain is indicated in simple outline, while the positions of the glands are indicated by shaded areas. For the purposes of diagram the Superior Palpebral Vein is omitted. It runs from the upper anterior part of the Orbital Sinus above the Maxillary Vein and joins the Inferior Palpebral Vein as the latter enters the Orbital Sinus. In dissecting out the vessels of the orbit it is almost always removed with the upper eyelid.

34. A First Account of the Courtship of the Redshank (*Totanus calidris* L.). By JULIAN S. HUXLEY, Lecturer of Balliol College, Oxford.

[Received February 2, 1912: Read April 23, 1912.]

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I. INTRODUCTION.

While staying last spring in a lonely corner of North Wales it was my good fortune to come across a number of rare and interesting birds. But great as was the pleasure of seeing, for the first time, such comparatively uncommon species as the Grey Plover and Black-tailed Godwit, it was far surpassed by that of being able to study, under the most favourable conditions, the natural behaviour and home life of some of the commoner shore-birds. Of these I was particularly fortunate with the Redshank,

and was able to see the whole of the courtship and pairing. When I say the whole, I do not mean that I saw every detail, nor that every detail I saw is clear to me. But I mean that I know what is the general course of events, and can interpret the birds' behaviour more or less consistently.

On returning to civilization and libraries, to my surprise I could find very little on the subject: the observations recorded were either fragmentary or inaccurate. It was not until most of this paper was written that I discovered a fairly complete account by Selous*. This had remained undiscovered owing to the absence of any reference to Redshanks in the title of the paper or in the index of the volume.

I have thought it worth while to publish my observations, however, since they differ in several points from those of Selous. Meanwhile, I fully realize their incompleteness, and recognize that they cannot as yet be properly used in any general discussion of the theory of sexual selection. I hope to continue my own observations when opportunity offers, but venture to publish this general outline at once as a stimulus to other bird-watchers and naturalists.

2. LOCALITY, etc.

Before passing on to the birds' actions I must first just mention the theatre where I saw them played. This was part of a small estuary in the northern half of Cardigan Bay: an arm runs out on one side at right angles to the river, thus giving during high spring tides a land-locked sheet of water nearly a mile long and half a mile wide; during neaps, even high tide failed to cover it. Numbers of Redshanks and other birds frequented this expanse, and especially its head or most landward end, where they were close to a thick bed of reeds and tussocks; the mud here was scarcely ever covered by the tide, though kept always moist by a little stream.

At one side of the head was a low ridge of grass-covered dunes, about five feet high and thirty or forty feet long, with level ground behind them. Thus, by crawling over the flat, I could get up to the dunes into an excellent position for viewing the whole top of the bay; every bird was easily seen against the wet mud. So I kept watch with the naked eye until some disturbance or unusual behaviour attracted attention; then, being armed with a telescope magnifying 30 diameters (for the loan of which I have to thank my brother, Mr. N. T. Huxley), I focussed this on the spot, and could see the minutest details of attitude and behaviour in the nearer birds, and even in those on the far side of the bay could quite well interpret what I saw. I made a number of notes on the spot, and usually within twenty-four hours embodied what I had seen the day before in a letter to an ornithological friend.

* E. Selous, "Observations tending to throw light on the Question of Sexual Selection in Birds," etc., Part I; *Zoologist* (4) x., 1906, pp. 201-210.

3. THE COURTSHIP PROPER.

I will begin with an account of the typical course of the courtship and pairing, such as I have seen repeated, with but slight variations, a considerable number of times.

Among the forty or fifty birds that usually would be quietly feeding on the flats, walking or running in short starts from mouthful to mouthful, a disturbance would every now and then be visible—two birds running, one pursuing the other. These two are cock and hen. A cock takes a fancy to one of the hens, leaves his feeding, and starts running towards her. She at once runs away from him, and there ensues a regular game of follow-my-leader. The hen never goes far in a straight line; she usually runs in a series of curves, often doubling sharply back, and sometimes describing a complete circle or even a figure of eight. Where she goes the cock goes after her, following exactly, but some yards behind. The couple would be ridiculous enough in their devious course, with heads somewhat down and quick-moving legs—rather the action of a fast-trotting horse—but the attitude of the cock adds to the effect: his eyes being set on the sides of his head, his neck has to be stretched stiff out and markedly sideways (at an angle of at least twenty degrees with the line of his body), in order to keep the hen in sight. In addition he spreads his pure white tail, so that you see half the fan of it on either side of the tips of the folded wings; but whether the hen so far ahead can see anything of this I do not know.

This pursuit goes on often for quite a long time, the birds covering maybe a quarter of a mile. The hen usually flies away, leaving the cock disconsolate, but sometimes she will consent to inaugurate the second stage of the courtship, in which she is able to inspect the suitor more closely. This she does by suddenly coming to a dead stop. The cock then perhaps runs a yard or two further, but soon he too stops, and begins his part of the second stage of the courtship.

The first stage was almost mere pursuit: the second is pure display. He first unfolds his wings and raises them right above his back, so as to expose their conspicuous under-surface of pure white somewhat clouded or barred with grey. Then, fluttering them tremulously, but keeping them raised all the time, he advances very, very slowly towards the hen, lifting his feet high in the air, and often putting them down scarcely in advance of where they were before. To the human eye the whole action seems the expression of eager excitement tempered by uncertainty, and that, presumably, is what the bird is actually feeling. Meanwhile, as he steps on, he stretches his neck a little forward, opens his mouth, and gives utterance to a single continuous note, which is changed into a long roll or rattle by the quick vibration of the lower mandible. The sound is quite like that of a Nightjar, but higher, and without any of the little breaks in the pitch of the note. So he advances closer and closer, the hen usually

remaining motionless. Again at any time during this stage she may reject his suit by flying off, but if she is going to accept him, she simply stays still, often without moving a muscle the whole time.

As the cock gets closer, he gets more and more excited, vibrates his wings more and more rapidly, at length so fast that almost his whole weight is supported by them, though he still continues to execute the high-stepping movements with his feet. At last, when just behind the hen, he abandons the ground, and flutters up on to her back, on which he half alights. The period while he is thus on her back is the third and last stage of the courtship: it is very short, and is of course in a sense nothing more than getting into the proper position for the actual pairing. But it should still be called part of the courtship, for even now the cock is not assured of his desire. Sometimes the hen, suddenly repugnant, or annoyed by the series of shriller, less continuous cries which the cock is now uttering, gives a violent jerk or sideways twist, and shakes him forcibly off on to the ground, herself running or flying away.

Occasionally, however, she apparently is satisfied; she spreads her tail diagonally, and the cock, with a quick and wonderfully graceful motion, half supported all the time by his fluttering wings, accomplishes the act of pairing. Then the hen gives the same violent twist that I have just mentioned, he gets shaken off, and they both begin quietly feeding, often side by side, but now no longer taking the least interest in each other.

That the course of true love should run so smooth was, however, quite the exception. Though I did not keep a record of the number of unsuccessful cocks that came under my observation, there must have been at the lowest estimate fifty of them, while but three times did I see the courtship consummated. Thus in something well over 90 per cent. of the cases I saw, pairing did not take place; and this was always due to the rejection of the male by the female, as the cock, once he had started a pursuit, never of his own accord abandoned it. Thus, though the hen does not actively select her mate from among a bevy of competing cocks, yet, like the modern European woman, she has the power of saying yes or no to each individual male who may choose (here literally, there metaphorically) to run after her.

The hen may reject her suitor at any time during the whole proceeding. On the one hand, I have seen her break off the courtship after a few seconds, while on the other I have seen her stop still after running, stand and watch the cock's display and gradual approach, even let him fly up on to her back, and only then with a sudden jerk throw him off and take to flight. Between these extremes there were, of course, all intermediates. During the first or pursuit stage, rejection was accomplished by the hen simply taking wing and flying off some fifty or a hundred

yards. The cock sometimes (though not usually) flew after her, settled, and began his running once more; but then she would very soon fly off again, and I never saw a cock persevere after a second such repulse. The first stage may be very short, as I have said, owing to her rejecting her suitor at once; and it may be short for the reverse reason, the hen stopping almost at once to let the cock come up for inspection. Usually, however, it is of considerable length, and in well over half the number of cases it ends in the rejection of the cock and the cutting short of the courtship before the second stage is reached.

Of the minority who survived thus far, a still larger percentage were rejected before getting to the third stage. This was most often accomplished by the hen simply flying off, leaving her suitor to fold his wings and pretend nothing had happened. Sometimes, however, if more undecided, she would behave in a curiously human way. As the cock got close she would as it were lean away from him, and at last, giving a little quiver all over, break into a short quick run of about four or five steps, like a frightened horse shying across the road. Then she stood still again, and, when the cock advanced again, very likely repeated the action. Of the five or six hens I saw act thus, all as a matter of fact at length flew off; but I have no doubt that occasionally they make up their minds in the opposite way.

4. OTHER HABITS OF THE PAIRING-SEASON.

There are other habits of the pairing-season which call for special remark. I do not understand their relations to the courtship proper, and shall merely mention them here. They are introduced partly for the sake of completeness and partly to show what a number of unsolved problems still exist concerning the habits of common birds.

(a) *The Love-flight*.—This is a well-known habit. A Redshank (presumably a cock) rises up into the air and there flies in a series of switchbacks. I will quote from my own notes on a particular bird: "Just before the bottom of each switchback he gave very quick wing-flaps, almost fluttering, one would call it; this made him start up again. He went on fluttering or flapping till he was about half-way up, and for the rest of the up-stroke of the switchback he soared up with the impetus he had gained. His wings now were set back and down, his neck and head thrown up in a beautiful proud attitude, his tail spread out. Then he turned the angle of his wings and glided down, still in the same attitude." While flying thus, he gives vent to what one may well call a song—a series of pure sweet single notes, never uttered on other occasions. The flight may be quite short, or may go on and on for several minutes. It is usually, I think, gone through by single birds, but I have fairly often seen it done

by one of two or one of three birds. If so, however, it was hardly ever repeated more than a very few times. I have several times seen it take place when I have frightened a bird up from feeding.

The meaning of this habit is hard to discover, and its relation (if any) to the courtship proper is equally obscure. It is performed, I believe, only in the spring, and would certainly seem to be of the same nature as the drumming of the Snipe or the short soaring flight of the Wood-Pigeon.

(b) *The Combats of the Males*.—These have been well described by Selous (*loc. cit.*). I agree with his opinion that the combats of many birds are now at least merely formal. This was well shown in the Redshank; the birds scarcely ever touched each other, and often did not even seem fierce. It was mostly a mere running up and down of two birds facing each other, often with a very formal-looking character about it. Further observation alone can reveal its significance.

(c) *Calling from a conspicuous perch*.—This is mentioned by various writers, and is a very noticeable custom. A single bird will settle on a gate-post, railing, notice-board, or other prominent perch, and will sit there, moving its head from side to side, and uttering a single note many times repeated. Usually after every few notes there comes a short pause. Long pauses are rare. One bird continued calling thus from the same perch for 45 minutes, and was still going on when I had to stop watching. I have at present no idea as to the sex of the calling bird, or as to the purpose of the whole proceeding.

5. DISCUSSION.

I will confine myself in this paper to a short discussion of the courtship proper, and will begin by comparing my observations with those of Selous (*loc. cit.*); all other descriptions can here be left out of account, owing to their vague and fragmentary character.

Selous, who made his observations in Holland, seems, to start with, to have seen a greater proportion of successful courtships than I did. His description (often hard to follow, as there is no arrangement—only notes in chronological order) differs in the following chief points from mine:—

1. He seems to have seen only two examples of the first stage of the complete courtship (pp. 212, 213), which is curious, since the follow-my-leader evolutions of my birds were most conspicuous.

2. His first stage is described as follows:—"The male, approaching the female, ran about her twice or thrice, in so many half-circles, fanning his tail as he did so, and inclining his body towards her." . . . That is to say, the hen was stationary,

instead of leading the cock a long chase, as in the Welsh birds.

3. Sometimes directly after pairing there was a curious set run or antic of the couple, *e. g.* (p. 206):—"Two Redshanks, after pairing, run, in an excited and curious-looking manner, over the sand, following one another." Another time (p. 204), (in perhaps slightly different circumstances):—"the birds walked, for a little, about and very near each other, fanning out their tails, whilst bending them inwards, so that, had their legs been short, they would have swept the ground at intervals, as does that of the courting pigeon."

4. He sometimes saw a male which had been definitely rejected begin courting the same female again after a short time, once or twice successfully; I never saw this happen. (This is presumably an error of omission on my part.)

These are the chief differences. His observations on the second and third stages and on the pairing itself are very similar to mine.

The differences may be ascribed either to real differences of behaviour of *Totanus calidris* in different parts of its range, or to errors or omissions of observation. Further watching alone will reveal the truth.

Further watching too must elucidate the following points, all of which ought to be known before a full discussion of the facts and of their bearing on the theory of sexual selection can take place:—

1. How often does each bird go through the act of pairing?
2. Is pairing promiscuous, or do birds pair for the season, or for life?
3. What is the relation between pairing and nest-building, and between pairing and each act of oviposition?
4. When does pairing begin in the spring, and for how long is it continued?
5. What is the relation of the love-flight, the combats, and the calling from a perch, to the courtship proper?
6. Does the female, who possesses all the structures used by the male in his display, ever use them herself for "showing off," or for any other purpose (recognition signals, etc.)?

With regard to 1, it is interesting to note that when the air was calm the Nightjar-like note described above (p. 649) could be heard at every hour of the night and day; on some nights there were one or more birds giving utterance to it practically all the time that I was listening. Now I am prepared to assert that this call is only used during the second stage of the courtship, so that the number of courtships which advanced as far as the second stage must have been very great (yet less than the number of those which never reached the second stage at all; *cf.* p. 651.)

The number of Redshanks near the head of the estuary (where alone they really congregated) was never very large. I should put fifty as an outside limit, and from observations on this and other species (*e. g.* Oyster-catchers), I believe that they are the same individual birds day after day. Therefore, even allowing that only a fraction of the courtships which reached the second stage were consummated, yet the number of acts of pairing must have been many times greater than the number of birds; probably, therefore, each bird pairs several times a day.

It is thus likely, as Selous says, that the performance of the courtship will vary very much in different circumstances; there may be satiety or eagerness in either sex, as well as timidity and shyness in the female, at different times. Selous adduces the Pheasant to prove that the display of the male may be gradually much abbreviated and scamped after the first few pairings.

As regards 4, I have very meagre evidence. I can only say that pairing had begun before the 8th of April, and was still going on very vigorously when I left Wales on the 18th. All the other questions I must leave for the present unanswered.

Selous' and my observations, however, are in themselves enough to establish one important point, namely, that the actions of the birds which lead up to each single act of pairing are explicable only on the Darwinian theory of Sexual Selection, or on some modification of that theory.

On the one hand, there is a very marked *display* by the male: the fanning of the tail in the first two stages, the lifting and fluttering of the wings, and the high-stepping with the legs in the second stage, are all obviously calculated to show off to the best advantage certain conspicuous markings which are usually concealed, while the rattling note of the second stage is to my mind equally to be considered as an excitant.

On the other hand, there is an equally marked *power of choice* shown by the female; it is perfectly clear that if a female Redshank does not want to pair with any given male, he has no possible means of forcing her to do so. He can only persuade her, or rather attempt to persuade her (by means of his display), and if she is very unfavourable to his suit, she can even prevent him from doing this, by flying off directly he begins.

Thus, though the male in this particular species has the *initiative*, the *final decision* must rest with the female.

The chief postulate of Darwinian Sexual Selection therefore holds good in the case of the Redshank:—The females have a power of choice, and the cocks have to go through a display before pairing. Moreover, the one certainly seems to stand in a causal relation to the other.

It is interesting to note, however, that although Sexual Selection is at work, yet it has not produced any appreciable difference between the sexes. This can be explained in one of three ways.

(1) The markings used in display (red legs, white tail, and whitish under surface of wings) were acquired previously by the species for some distinct purpose (*e. g.* as recognition or obliteration markings) or possibly accidentally, and then were turned to account by the cock as the "physical basis" of his display. The hen would of course possess the markings too; she differs from the male in not having secondarily acquired the instinct to display them.

(2) The markings were acquired by the cock first or primarily as secondary sexual characters, to form the basis of his display, but were either at once or later found to be of use in other ways: they would then tend to be transferred to the hen as well, either from their first beginnings, or subsequently to their definitive development in the cock, by the operation of Natural Selection.

(3) The markings were acquired for purposes of display, while in other respects they are neither harmful nor the reverse; the instinct to use them for display, however, depends on a physiological stimulus only present in the male sex. Then they would tend to be transferred to the female sex, for we generally find that the two sexes resemble each other unless there is some definite reason for their differing. It appears to be both more primitive and easier for hereditary characters to be transmitted equally to both sexes.

It is at present very hard to decide between these possibilities. Of the three, the last appears the least probable. What does emerge clearly, however, is that in considering the facts of Sexual Selection, as so often elsewhere, we must be careful not to isolate structure from function. When we speak of secondary sexual characters, we usually think of structures only. In reality the real character is the structure plus the instinct to use the structure, for it is the *use of the structure* which alone has any significance for the species: it is that which constitutes a unity, it is that which has been really acquired by the species. For purposes of convenience we separate it into two components—structure and function; but in any question of its origin and history we must always be careful to think of it as a whole. To take a concrete example: if it were proved (as is probable) that the female Redshank never used her white tail, etc. for purposes of display, we should be justified in saying that the Redshank showed secondary sexual characters—these characters being the various *actions of display* found in the male, and in the male alone.

This point of view will perhaps help to make more intelligible the various cases which have been described where the sexes are alike in plumage, but the male alone goes through a display.